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The Energetic Consequences of Temperature Variation and Sequential Autotomization for the Stone Crab, Menippe spp.

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by

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ABSTRACT

The stone crab, *Menippe* spp., is harvested in a claw only fishery along the Gulf and southeastern Atlantic coasts of the United States. As climate change continues to warm these areas, crabs are forced to cope with higher water temperatures and lower dissolved O_2 concentrations. These altered environmental conditions may influence crab energetics by altering both energy intake and expenditure. To inform fishery sustainability as well as prepare for a potential range expansion of the crab, this study investigates the energetic intake and expenditure of individual stone crabs. Crabs were found to respire 80 and 69% more following the loss of major and minor claws, respectively. The Q_{10}, the factor by which the mass-specific respiration rates change as the temperature is increased by 10°C, was found to be 1.536. Mortality as a result of first and second claw loss were 6.25 and 13.3% when using stimulated sequential autotomization. Consumption of oysters in field cages increased by 15.8% of the crabs' weight for every 10°C increase in water temperature. Ingestion efficiency did not significantly vary with crab size, water temperature, or claw loss. I hypothesize that the ingestion efficiency of soft tissue did not change with the loss of the claws due to the unique feeding behavior of the stone crab. The front four walking legs were used more in food manipulation than both major and minor claws. Although current regulations were designed to promote the reentry of previously harvested crabs to the commercially available stock, the results of this study suggest stone crabs may struggle to cope with

fishery-style claw loss in warming conditions expected with continued climate change, especially in areas that are O_2 depleted.

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CHAPTER 1

INTRODUCTION

The world's oceans are experiencing increased water temperatures due to global climate change (Bindoff et al. 2007). Over the past 100 years the global mean surface temperature has risen by approximately 0.6°C and is projected to continue rising for several centuries (IPCC 2001). Although regional climate patterns are often dynamic and heterogeneous (Burrows et al. 2011), this study focuses on the western north Atlantic along the U.S. coast where ocean warming is projected to be among the strongest in the world (IPCC 2013). The temperatures within a region influence the ecological processes that occur there, such as mortality (Hallett et al. 2004), nutrient cycling and productivity (Allen 1995), as well as specifics of both animal behavior and physiology (Holtby 1988). Ectotherms are particularly sensitive to temperature changes because of the influences on individual development, energetics, physiology, and behavior in this group of organisms (Precht et al. 1973; Wieser 1973).

Temperature shifts associated with climate change have caused many marine ectothermic organisms to begin shifting their ranges towards the poles (Southward et al. 1995; Walther et al. 2002; Helmuth et al. 2006; Last et al. 2011). However, range shifts are often hard to quantify. For marine invertebrates Cheung et al. (2009) reported an average rate between 45 and 59 km per decade whereas Burrows et al. (2011) reported

the rate between 14 and 38 km per decade. Rather than only studying the rate at which a species may shift its range, it is important to understand the energetic processes that drive an organism's physiology throughout a range of temperatures. Such a mechanistic understanding enables us to better describe a species' response to climate change throughout its range and may also help us to understand potential range shifts. This understanding may be particularly important for commercially harvested species. The regulations and harvesting zonations of a fishery are often indirectly determined by the temperature ranges that dictate where harvested species are successful (Mellin et al. 2012). Shifts in a commercial stock's range or physiology could lead to a need for altered regulations or a shift in the primary location of the fishery.

One commercial stock that appears to be experiencing a poleward range shift is the Florida stone crab, *Menippe mercenaria*, and Gulf stone crab, *Menippe adina* (Rindone & Eggleston 2011). Stone crabs are managed as one species in commercial fishing and are therefore treated as a single species in this study. These crabs are naturally found in the North Atlantic from North Carolina to Mexico and throughout the Caribbean (Bert 1986). While the fishery within the U.S. exists in all coastal southeastern states in some capacity, it is most prominently found on the west coast of Florida which has accounted for 97.1% of landings since the 2000-2001 season (NMFS 2016). However, the Florida stock is currently listed as fully exploited and a surplus production model has concluded that it is overfished in each of the last four stock assessments (Muller et al. 1997; 2001; 2006; 2011). Additionally, the landings for both the 2014-15 and 2015-16 seasons are the lowest since 1976-77 (NMFS 2016). Recently, fishermen have reported higher abundances of stone crabs in waters previously thought to be north of the crabs'

natural range (Rindone & Eggleston 2011), and the commercial landings in North and South Carolina have increased in recent years (NMFS 2016) suggesting the beginning of a poleward range shift.

Understanding the physiological performance for this stock is particularly important not only due to the species' range shift, but also because it is harvested in a claw-only fishery. Claw-only fisheries aim to lessen the impact on populations by harvesting only the claw(s) and releasing the individual with the expectation that the lost claw(s) will be regenerated so that the crab can reenter the fishery. However, analysis of stridulation ridges (Simonson 1985) show long term trends of regenerated claws representing only 9.5-13% of total Florida landings (Savage et al. 1975; Muller et al. 2006; Muller et al 2011). These results suggest many stone crabs may not be able to contribute to the fishery a second time. The low landing rates of regenerated claws can be attributed to numerous factors. First, the fishery technique used to remove claws often results in breaks not along the natural autotomy-fracture plane causing wounds correlated to mortality (Davis et al. 1978; Simonson & Hochberg 1986). Also, adult stone crabs are generally only able to regenerate a lost claw to its previous size or greater after two or more years in ideal conditions (Savage and Sullivan 1978; Restrepo 1989). However, a two-year regeneration period is not likely to occur before many crabs reach their terminal molt (Cheung, 1973). Furthermore, regeneration frequencies are lower in field populations (Savage et al. 1975). Claw regeneration to the size of fishery eligibility likely requires major energetic investment (Niewiarowski et al. 1997; Naya et al. 2007) and, due to the ectothermic nature of crabs, may be strongly reliant on the crabs' temperature-dependent energetic processes.

To fuel these energetic processes, the crabs must eat. The primary diet for adult stone crabs is hard-shelled bivalves (Gunter 1955; Menzel & Nichy 1958), however, Hogan & Griffen (2014) found that 1-clawed stone crabs consume 50% fewer bivalves than those with 2 claws. Similarly, feeding on hard-shelled bivalves was virtually eliminated for *Cancer pagurus* after claws were autotomized. Autotomized *C. pagurus* also demonstrated significantly higher consumption of fish flesh compared to 2-clawed individuals (Patterson et al. 2009). Although fish flesh consumption has not been quantified with clawless stone crabs, Bender (1971) suggested they are able to alter their diet to consume more macroalgae after claw loss. Hogan & Griffen (2014) found no evidence to support this claim but did find stone crabs would consume polychaete worms regardless of the number of claws present. This suggests the potential ability of stone crabs to shift to another primary carnivorous diet after claw loss given the tissue is readily available. Regardless of food type, ingestion efficiency has rarely been studied in any crab species with or without the influence of claw loss. Additionally, the influence of temperature on consumption rates and ingestion efficiency has yet to be addressed for stone crabs. Since most crabs use exclusively claws in feeding (Elner & Hughes 1978; Smallegange & Van Der Meer 2003) it is logical to assume that ingestion efficiency, like consumption rates (Hogan & Griffen 2014), would decline when the claws are removed. Stone crab feeding behavior has not yet been quantified to investigate this potential mechanism of decreased consumption and efficiency. The compensatory use of walking legs has been observed to open and manipulate oysters when stone crabs are missing claws (Savage & Sullivan 1978). The reduced energy intake associated with potentially

altered diets or decreased ingestion efficiency may impact the energetic processes dictating claw regeneration.

To inform the sustainability of current regulations and to prepare for the expected continued range shift of stone crabs, I aim to understand the individual energetics and feeding processes of these crabs. In this study I tested the following hypotheses: 1) the stone crabs' respiration rates will increase with temperature, claw loss and crab size; 2) food consumption will increase with claw loss when soft-tissue is readily available; 3) the consumption of bivalves will increase with temperature and crab size; 4) the ingestion efficiency will increase with respect to temperature and crab size, and decrease with claw loss; and 5) the use of walking legs in feeding behavior will increase with claw loss.

CHAPTER 2

MATERIALS AND METHODS

I conducted five experiments. The first experiment examined the influence of sequential autotomization on mortality and how respiration rates changed (acclimated) over a 3-week time period in the lab, with and without the influence of claw loss. The second examined the influences of temperature variation and sequential autotomization on respiration rates. All crabs used in the first two experiments were collected from the Stono River in Charleston, SC (32°45’31” N, 80°00’16” W). The third experiment examined the influence of temperature variation on the consumption of oysters in field cages. The fourth examined the influences of temperature variation and sequential autotomization on ingestion efficiency in the lab. The fifth experiment quantified feeding behavior of the stone crab on single oysters to investigate the mechanistic use of walking legs versus claws. All crabs used in the third, fourth, and fifth experiments were collected from Town Creek in the North Inlet-Winyah Bay National Estuarine Research Reserve near Georgetown, SC (33°19’57” N, 79°11’17” W). Stone crabs in these two areas are generally hybrids of *Menippe mercenaria* and *Menippe adina* (Bert 1985), but I did not distinguish between these species or hybrids for the purposes of this study. Also, approximately 38% of the stone crabs in the first two experiments and 39% of the crabs in the last three experiments had left-handed crusher claws, similar to what has been previously reported (Cheung 1976). Stone crabs are naturally right-claw dominant (Cheung 1976, Davis et al. 1978), becoming left-claw dominant only after claw loss. I

included both left- and right-handed crabs haphazardly in the following experiments. All data analyses were performed in R (R Core Team 2016).

Mortality & Acclimation Experiment

I collected a total of 16 legal-sized stone crabs during the summer of 2015 (6 females and 10 males; CW ± SD, 89.5 ± 6.35 mm) for use in the first experiment. The crabs were transported to the University of South Carolina and placed in recirculating tanks of approximately 0.155 m^2 at 25±0.5°C. Tanks were supplied with a ASM G-2 in-Sump protein skimmer and live rock to maintain water quality. A 10x30.5 cm PVC pipe was provided to each crab for use as a false burrow (Beck 1995). I fed each crab 20 grams-wet mass of tilapia (*Oreochromis* spp.) every other day. Crabs were split into two blocks for feeding, with half of the crabs being fed on any given day. Crabs were given 4 hours to consume this food before any uneaten food was removed. The respiration rates described below were measured 24 hours after feeding, ensuring that these measurements reflected resting rates and not specific dynamic action (Secor 2009).

Crabs were split into 2 treatments – experimental crabs that sequentially lost their claws throughout the experiment, and control crabs that retained both claws throughout the experiment. The sequence of the experiment proceeded as follows. After an initial minimum 6-day acclimation period I observed 4 crabs per day (2 experimental and 2 control) in respiration chambers until all 16 crabs had been observed. Respiration chambers consisted of an air-tight 12.2-liter tank that was filled with sea water and partially submerged in a water bath at 25°C. Water in the experimental chamber was mixed throughout the measurement period using a magnetic stir bar located below a perforated subfloor so as to not disturb the animal whose respiration rate was being

measured. After placing a single crab into the chamber, I measured dissolved O_2 (ppm) every 10 minutes for 2 hours using a Hanna Instruments HI9146-10 dissolved O_2 meter. Crabs were fed, according to their normal feeding schedule, immediately after these respiration measurements. Following this feeding period, I triggered autotomization of crabs in the experimental group by applying mechanical stress until they autotomized the larger, crusher claw. To induce autotomization through mechanical stress I clamped the merus and applied repeated point pressure just beyond the coxa. I used this method rather than traditional declawing methods used by the fishery in order to reduce injuries that may lead to mortality (Davis et al. 1978). Mortality measured in this experiment is therefore not representative of the declawing methods of the fishery but rather the minimized injuries caused by natural autotomization. I gave the crabs 7 full days after autotomization to acclimate before being handled again, while continuing the regular feeding cycle during this time. On the eighth day, I again measured their respiration rates. This was followed by removal of the second claw, again by applying mechanical stress until the crab autotomized its own smaller, cutter claw. I again gave the crabs 7 full days after autotomization to acclimate before being handled again, while continuing to feed them. This was followed by a final respiration rate measurement. Claws removed throughout the experiment were frozen for later measurements.

Following the experiment, I measured the volume of the body and each claw by water displacement. I used these volumes to account for water displacement by crabs in the respiration rate chambers. I then dried the body and each claw at 70°C for 5 days and determined their dry mass. The respiration rate for each 10-minute interval throughout each 2-hour measurement period was calculated and converted to ml O_2 g^{-1} dry mass h^{-1}

for analysis. I analyzed respiration rates using a mixed effects linear model with the number of claws, measurement week, and gender treated as fixed categorical factors, the initial O_2 concentration for each 10-minute interval and crab size were treated as continuous variables, and crab ID treated as a random factor to control for repeated measurements of the same individuals.

Temperature-Respiratory Experiment

I collected a total of 32 legal-sized stone crabs during the summer of 2015 (10 females and 22 males; CW ± SD, 91.8 ± 6.48 mm) for use in the second experiment. The crabs were again transported to the University of South Carolina and placed in the same recirculating tanks as described above. However, in this experiment, all crabs experienced sequential autotomization and water temperature was manipulated as the experimental treatment and was maintained at approximately 15, 20, 25, or 30°C. Eight crabs were used at each of these four experimental temperatures, and temperatures in each tank were constantly maintained within 0.5°C of the target values. All other aspects of the experimental setup and maintenance were identical to those described above. However, in this experiment I also quantified the amount of food consumed in order to determine how claw loss and temperature influenced the consumption of fish flesh. At the end of each 4-hour feeding period, the uneaten food was collected, dried at 70°C for three days, and weighed in order to determine amount consumed.

As with the first experiment, I held crabs for at least 6 days of acclimation before observing 8 crabs per day (2 from each temperature) in respiration chambers until all 32 crabs had been observed. Respiration chambers were the same as described in the above experiment, the water bath temperature corresponded to the holding tank temperature so

that individual crabs experienced the same constant temperature throughout the duration of the experiment. I conducted respiration rate measurements and triggered claw loss as described in the first experiment.

Following the experiment, I measured the volumes and dry mass of the body and each claw as described in the previous experiment. I calculated the respiration rate for each 10-minute interval throughout the 2-hour measurement period and converted this to ml O_2 g^{-1} dry mass h^{-1} for analysis. I analyzed respiration rates using a mixed effects linear model with the number of claws and temperature treated as fixed categorical factors, with the initial O_2 concentration for each 10-minute interval treated as a continuous variable, and with crab ID treated as a random factor to control for repeated measurements of the same individuals. I used z-scores ($\frac{x-\mu}{SD}$) to scale water temperature and initial O_2 concentration. The use of z-scores allowed us to make direct comparisons from the linear regression between the parameter estimates for different explanatory variables, but did not influence the t-values or p-values. The Q_{10} was calculated using the equation, $Q_{10} = \left(\frac{R_H}{R_L}\right)^{\left(\frac{10}{T_H - T_L}\right)}$ where T_H and T_L were the average high and low temperatures during the 2-hour measurement period and R_H and R_L were the average respiration rates measured at the high and low temperatures. Since the respiration rates varied with initial O_2 concentrations and the initial O_2 concentrations varied with temperature, the average R_H and R_L values were only calculated from the 10-minute intervals whose initial O_2 concentrations were found at each of the temperatures. I analyzed consumption rates of tilapia using a mixed effects linear model with the number of claws and temperature treated as fixed categorical factors, with the crab size treated as

a continuous variable, and with crab ID treated as a random factor to control for repeated measurements of the same individuals.

Consumption Experiment

I collected a total of 41 legal-sized stone crabs between October 22nd, 2015 and September 23rd, 2016 (13 females and 28 males; CW ± SD, 90.6 ± 11.6 mm) for use in the third experiment. Experimental periods consisted of seven separate week-long trials preformed between October 2015 and October 2016 (Table 2.1). The number of replicate crabs included in each trial varied based on the number of healthy stone crabs successfully captured prior to the start of each trial. During preliminary experiments with water temperatures as low as 15°C I observed drastically reduced feeding. Thus, I elected to not measure consumption rates during the winter months because water temperatures in the field reached weekly averages as low as 8°C. For each of the seven trials the sequence of the experiment proceeded as follows.

Crabs were held for a 24-hour starvation period in individual porous tanks (circular with diameter 26.24 cm; water height 30 cm) submerged in a flow-through tank (circular with diameter 1m; water height 30 cm), that was supplied with water from the estuary. Completely enclosed cages with dimensions 61 x 46 x 30.5 cm (length x width x depth) and 7 mm Vexar mesh were used for both experimental and control measurements. Experimental cages held a single stone crab, 3124.1 ± 122.1 g (avg. ± SD) of eastern oyster clumps (*Crassostrea virginica*), and a 10x30.5 cm PVC pipe for use as a false burrow (Beck 1995). Control cages held 3137.8 ± 161.5 g of oyster clumps and a 10x30.5 cm PVC pipe, but no crab. Oyster clumps were gathered from a tidal creek (33°21’53” N, 79°10’6” W), washed clean of mud, cleared of mud crabs (*Panopeus*

herbstii and *Eurypanopeus depressus*) and ribbed mussels (*Geukensia demissa*), sundried, and weighed to the tenth of a gram before placement in cages. Cages were then positioned at least 1.5 m apart and within 150 m of the Oyster Landing Station (NOAA Station ID: 8662245) such that at the lowest tide during the week-long experimental period, cages were still fully submerged under at least 30 cm of water. Following the week-long experimental period, cages were collected and crabs were immediately separated from oysters. All live oysters and shell fragments (≥7 mm) from both experimental and control cages were collected, washed clean of mud, sundried, and weighed to the tenth of a gram. The difference in oyster mass in experimental cages between the beginning and end of the experimental period was considered the amount of oyster consumed by the stone crab assuming 100% ingestion efficiency. The average difference in oyster mass in control cages was used as correctional value for experimental cages. A minimum of 3 control cages were present in each trial, and their mass differences (before – after) were averaged for a correctional value for each trial separately. Meteorological and water quality data were collected in 15-minute intervals for the duration of each week-long trial from NOAA Station 8662245 (NOS/CO-OPS 2016) and averaged for the entire week.

I analyzed consumption using a linear regression model with the water temperature, salinity, and crab mass as continuous variables and gender as a fixed categorical variable. Other water quality parameters were measured on site but were not used in the model based on strong covariance with salinity or temperature. I again used z-scores ($\frac{x-\mu}{SD}$) to scale crab mass and water temperature in the linear regression because the range of crab mass measured was over 33 times greater than the range of water

temperatures. The use of z-scores again allowed us to make direct comparisons between parameter estimates for different explanatory variables without influencing the t-values or p-values.

Ingestion Efficiency Experiment

I collected a total of 14 legal-sized stone crabs during the summer of 2016 (17 females and 9 males; CW ± SD, 93.5 ± 10.3mm) for use in the fourth experiment. The crabs were transported to the University of South Carolina and placed in recirculating tanks of approximately 0.31 m^2 held at either 18 or 28°C (temperature was consistently maintained within 0.5°C of the target value). Tanks were again supplied with an ASM G-2 in-Sump protein skimmer and live rock to maintain water quality. A 10x30.5 cm PVC pipe was provided to each crab for use as a false burrow (Beck 1995). In this experiment, all crabs experienced sequential autotomization; water temperature was manipulated as the experimental treatment.

After an initial 7-day acclimation and starvation period, I observed 4 crabs per day (two from each temperature treatment) in measurement tanks until all crabs had been observed. Measurement tanks were 32.4-liter flow-through tanks supplied with water at 10 liters per minute from the recirculating tanks used to hold crabs. Water leaving the measurement tanks was filtered through grade 50 cheesecloth to catch all food particles. After placing a single crab and single piece of tilapia (22.3 ± 2.16 g) into the tank, the tank was covered with an opaque plastic film to provide a dark environment and left undisturbed for 24 hours. Immediately following the end of the 24-hour measurement period crabs were removed from measurement tanks and tanks were drained through the cheesecloth filter. Any uneaten tilapia was washed from the measurement tank into the

filter. Filters and all food particles not ingested by the crabs were dried at 70°C for 5 days. Following the 5-day drying period I measured the total mass of all food with the filter, any uneaten food that was too big to have been carried away by the water current was then removed and weighed separately. Following the measurement period, I triggered autotomization as described in the first experiment. I gave the crabs 8 full days after stimulating claw loss to acclimate before being handled again. I did not feed crabs during this 8-day period. On the ninth day, I again measured the crabs' ingestion efficiency following the same protocol as the first measurement. This was followed by autotomization of the second claw using the same methods, and another 8-day acclimation period. This was followed by a final ingestion efficiency measurement period.

Efficiency calculations were performed as follows; $E_I = \frac{(T-(U+F))}{M} \times 100$ where E_I is the ingestion efficiency, T is the total mass of the filter and all food particles after drying and removing fecal pellets, U is the dry mass of uneaten food too big to have been taken by the water current, F is the mass of the filter, and M is the dry mass of the initial meat provided to the crabs. T, F and U were measured to 0.01g, and M was calculated as follows. I weighed pieces of tilapia (22.3 ± 5.15g) before placing them directly into the drying oven at 70°C for 5 days. After the drying period, I weighed the tilapia and formed a regression of the dry mass with respect to the wet mass (R^2=0.9681). I then used this regression to calculate the initial dry mass of tilapia from the initial wet mass. Mass of the food the crab attempted to eat was defined as the difference between the mass of the initial meat provided to the crabs and the mass of uneaten food too big to have been taken by the water current ($= M - U$). I analyzed ingestion efficiency using a general additive

model with carapace width and mass of the food the crab attempted to eat as smoothed parameters and temperature, number of claws present, and gender as categorical parameters. A general additive model was used to account for the nonlinear relationship between mass of the food the crab attempted to eat and the ingestion efficiency. Carapace width and mass of the food the crab attempted to eat were smoothed using a smoothing spline fit.

Feeding Behavior Experiment

I collected a total of five stone crabs during the fall of 2016 (2 females and 3 males; CW ± SD, 88.3 ± 11.1mm) for use in the fifth experiment. The crabs were transported to the University of South Carolina and placed in 12.2-liter individual holding tanks held at room temperature (approximately 22°C). Tanks were continually bubbled with air to maintain dissolved O_2 levels. All six sides of the holding tanks were transparent to facilitate observation. High definition video recordings of feeding behavior were collected using a GoPro Hero 4 video camera mounted underneath holding tanks directed up for a ventral view of each crab.

Crabs were fed a single oyster (avg. ± SD, 85.3 ± 10.7mm) overnight with a red lamp used to illuminate the camera's view and minimize any visual disturbance to the crab (Griffen & Williamson 2008). Each crabs feeding was recorded three separate times to observe variation within an individual. Analysis of video recordings proceeded as follows. Total handling time was recorded, in seconds, such that it began when the crab made initial contact with the oyster and ended once the crab no longer actively engaged with oyster shell fragments. The total time was then split into two categories; 'time eating' consisted of all seconds that the crab was actively manipulating or feeding on the

oyster while ‘time not eating’ consisted of all seconds that the crab was not manipulating and/or feeding on the oyster. The number of times each appendage (major claw, minor claw, or walking legs) was used was counted for ‘time eating.’ Each tally was defined by an appendage being used to independently manipulate shell fragments after the oyster had been opened. The major claw was often placed in front of the crab and used as a barrier to prevent shell fragments from sliding away; this was not counted as a manipulation in the tally because the major claw was motionless and did not manipulate oyster fragments. Counts for the front four walking legs were combined to compare claw verses walking leg use. I chose not to quantify the relative use of walking legs to manipulate food after crabs had autotomized one or both claws because walking legs were already used far more often than either claw when both were present. I analyzed the transformed number of times each appendage was used with a Tukey’s HSD test. The number of times used for each appendage type was transformed using a two-parameter Box-Cox transformation (Box & Cox 1964) to reduce variance in the appendage use. I analyzed handling time and time eating using mixed effects linear models with the crabs’ carapace width and oyster shell size treated as fixed continuous variables and with crab ID treated as a random factor to control for repeated measurements of the same individuals.

Table 2.1. Dates of week-long experimental periods from the consumption experiment. Temperature and salinity measurements were recorded in 15-minute intervals and averaged for the entire week.

Experimental Date		Temperature (°C)	Salinity	No. Males	No. Females
2015	Oct. 24-31	21.29 ± 1.03	31.28 ± 2.16	7	2
2015	Nov 14-21	17.78 ± 1.36	24.03 ± 3.10	6	3
2016	Apr. 23-30	23.74 ± 2.24	34.07 ± 0.48	4	2
2016	May 14-21	23.69 ± 1.22	34.29 ± 0.39	2	3
2016	July 8-15	30.94 ± 1.39	34.90 ± 0.36	1	3
2016	Aug 7-14	30.94 ± 1.33	33.98 ± 1.27	3	0
2016	Sept. 24-Oct. 1	27.65 ± 0.81	29.16 ± 3.74	3	2

CHAPTER 3

RESULTS

Mortality & Acclimation Experiment

Crabs that did not experience claw loss had decreasing respiration rates over the course of the experiment, suggesting acclimation to experimental conditions. Respiration rates independent of claw loss decreased 30% between weeks one and two ($p = 0.0002$) and 14% between weeks two and three ($p < 0.0001$). Conversely, the loss of both major ($t= 5.091$, $p < 0.0001$) and minor ($t = 3.682$, $p = 0.0003$) claws led to increased respiration rates. After correcting for decreases in respiration rates associated with time in the lab (using results from control crabs), major and minor claw loss lead to an average respiration rate increase of 80% and 69%, respectively (Figure 3.1). Changes in oxygen depletion increased 4×10^{-4} ml O_2 g^{-1} dry weight crab h^{-1} for every 1 ml O_2 L^{-1} increase in initial O_2 concentration ($t = 3.733$, $p = 0.0002$). Variation in respiration rates was high (SD = 7×10^{-5} ml O_2 g^{-1} dry weight crab h^{-1}). Mortality rates following sequential autotomization for first and second claw loss were 6.25% and 13.3%, respectively. Respiration rates were not significantly influenced by gender ($p = 0.2977$) or crab size ($p = 0.6195$).

Temperature-Respiratory Experiment

Mass-specific respiration rates increased with water temperature (Parameter Estimate [PE] = 0.0062, $t = 3.484$, $p = 0.0017$, Figure 3.2), initial O_2 concentration (PE =

0.0282, t = 6.353, p < 0.0001), and sequential autotomization (PE = 0.0223, t = 4.952, p < 0.0001, Figure 3.2). The Q_{10}, the factor by which the respiration rates change as the temperature is increased by 10°C, was found to be 1.536. Variation in respiration rates with initial O_2 concentration was high ($R^2 = 0.0058$). Mortality due to claw loss increased by a factor of 3.340 for each 10°C increase in water temperature. Mass-specific respiration rates were not significantly influenced by the crab size (p = 0.5373) or gender (p = 0.2532). Using z-scores the initial O_2 concentration and water temperature were found to have similar impacts on respiration rates (PE ± SE; 0.0330 ± 0.0052 for initial O_2 concentration and 0.0314 ± 0.0095 for water temperature). The consumption of tilapia increased with carapace width (t = 2.720, p = 0.0100) and claw loss (t = 2.435, p = 0.0155), but not temperature (p = 0.5971).

Consumption Experiment

Control cages exhibited a decrease in oyster mass. Consumption rates increased with water temperature (t = 4.229, p = 0.0002, Figure 3.3) and crab mass (t = 3.087, p = 0.0042, Figure 3.4). Consumption of oysters increased by 15.8% of the crabs' mass for every 10°C increase in water temperature ($R^2 = 0.5085$). Using z-scores the water temperature was found to have a nearly 2-fold greater impact on the consumption rate than the mass of the crab (PE ± SE = 103.8 ± 24.5 for water temperature and 54.9 ± 17.8 for crab mass). There was no significant change in consumptions rates with gender (p = 0.4786) or salinity (p = 0.9052).

Ingestion Efficiency Experiment

Ingestion efficiency increased with the mass of tilapia the crab attempted to eat (F = 4.121, p = 0.0460, Figure 3.5). Efficiency was not significantly different (t = 1.241, p =

0.2315) between 2-clawed (E_I = 80.44%) and 1-clawed crabs (E_I = 89.73%), however 0-clawed crabs did have a lower average ingestion efficiency (E_I = 46.92%) though the difference was not significant at α=0.05 (t = -1.766, p = 0.0955). There was no significant change in ingestion efficiency with water temperature (p = 0.2906) or crab size (p = 0.3860).

Feeding Behavior Experiment

The front four walking legs were used significantly more in food manipulation than minor claws (p < 0.0001) and minor claws were used significantly more than major claws (p < 0.0001, Figure 3.6). The back four walking legs were observed stabilizing the crab against the substrate when oysters were handled, never manipulating food. Total handling time was inversely related to carapace width (p = 0.0298) but did not significantly vary with oyster size (p = 0.7834). However, the proportion of the handling time defined as 'time eating' did increase with oyster size, although the relationship was not significant at α=0.05 (p = 0.0575). Individual variability in handling time was generally low, but was very high for a single crab (Figure 3.7).

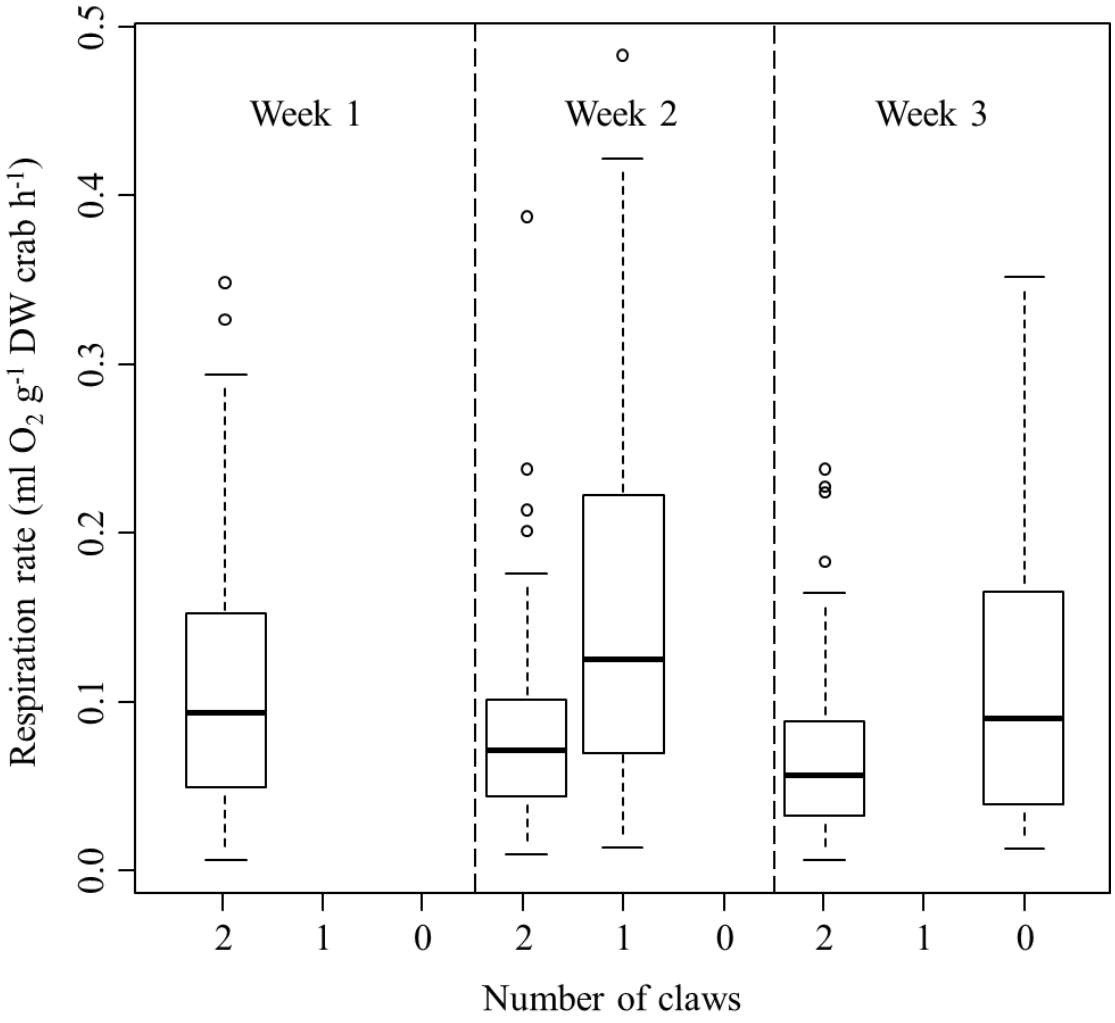

Figure 3.1. The mass-specific oxygen depletion by stone crabs in the mortality & acclimation experiment. In the first week, all crabs had both claws; experimental crabs lost their major and minor claws in weeks two and three, respectively, while control crabs retained both claws throughout. (The heavy line represents the median while the box gives the upper and lower quartiles. Whiskers encompass 95% of the data and circles are outliers.)

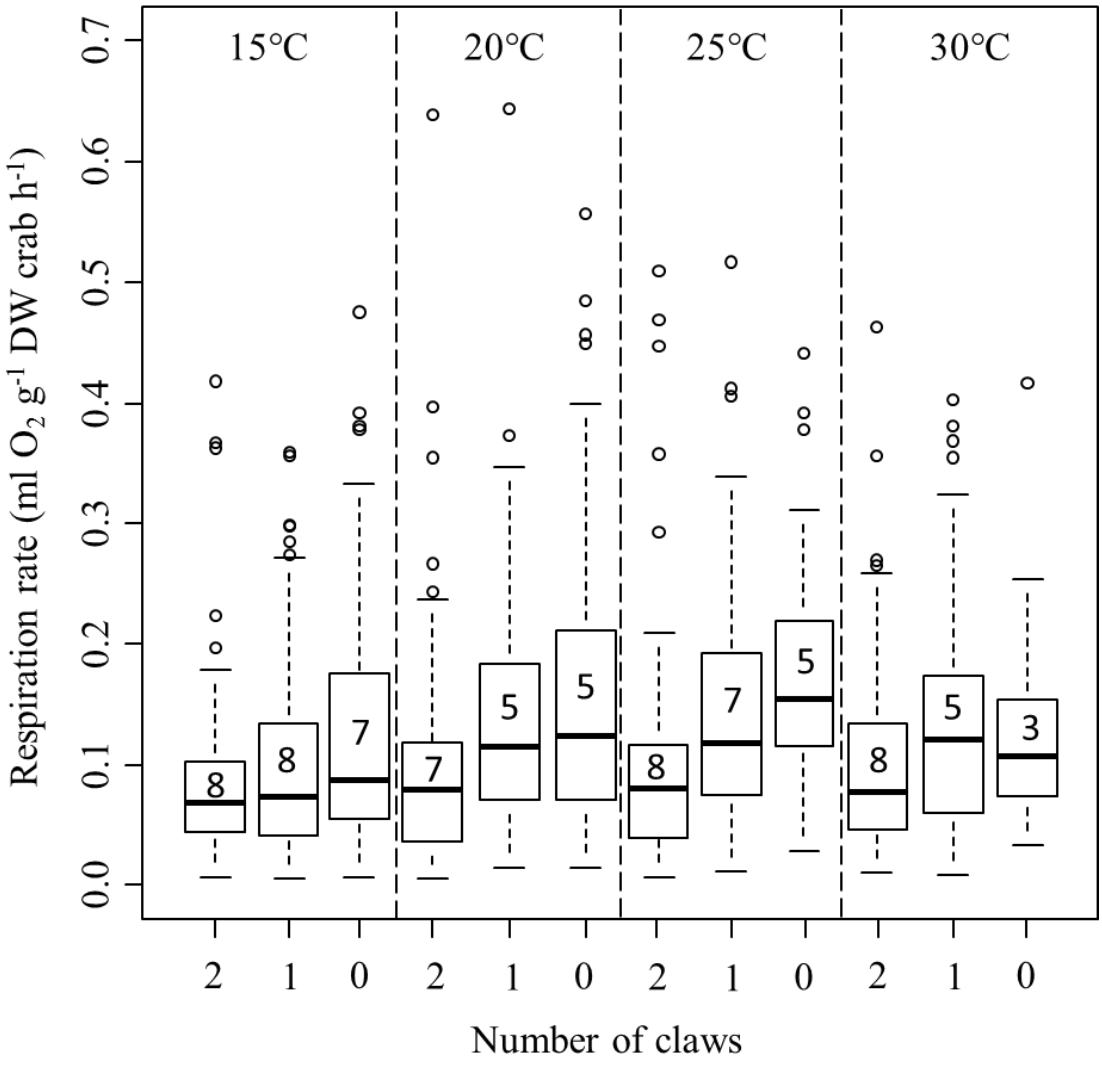

Figure 3.2. The mass-specific oxygen depletion by stone crabs in the respiratory experiment. The numbers inside the boxes represents the number of crabs measured at a certain number of claws and temperature (this number decreased throughout the experiment due to crab mortality).

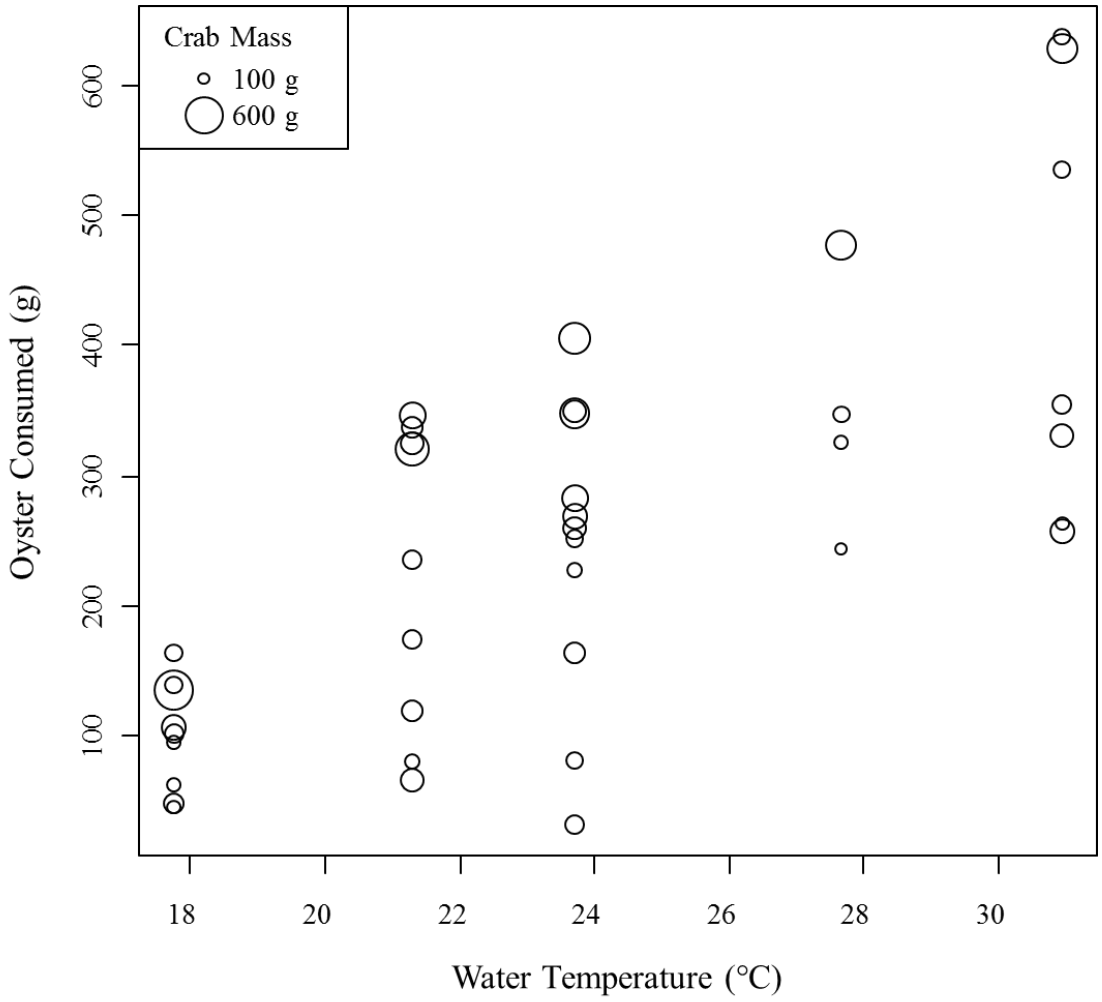

Figure 3.3. The consumption rates of stone crabs on oysters with the corresponding crab mass. Data points are scaled to the water temperature during the experimental period.

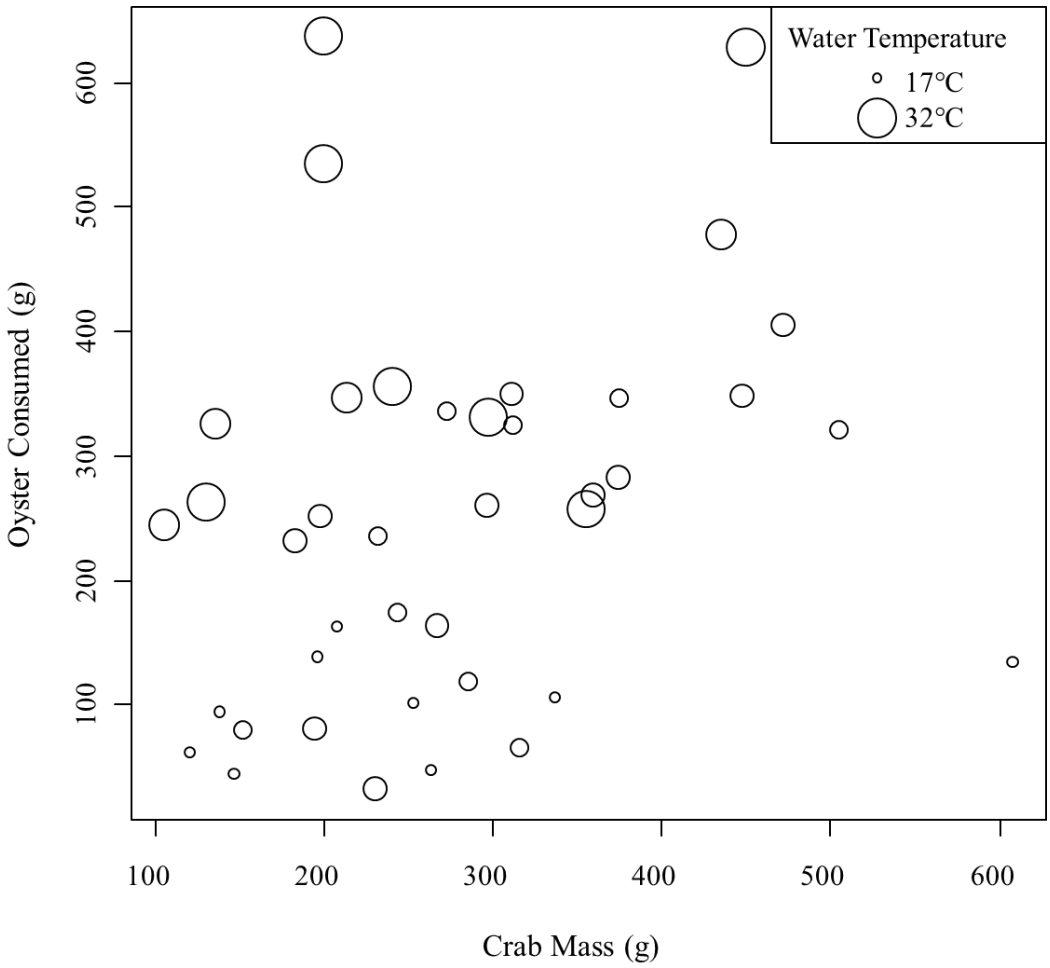

Figure 3.4. The consumption rates of stone crabs on oysters with the corresponding water temperature. Data points are scaled to the crab mass of each crab.

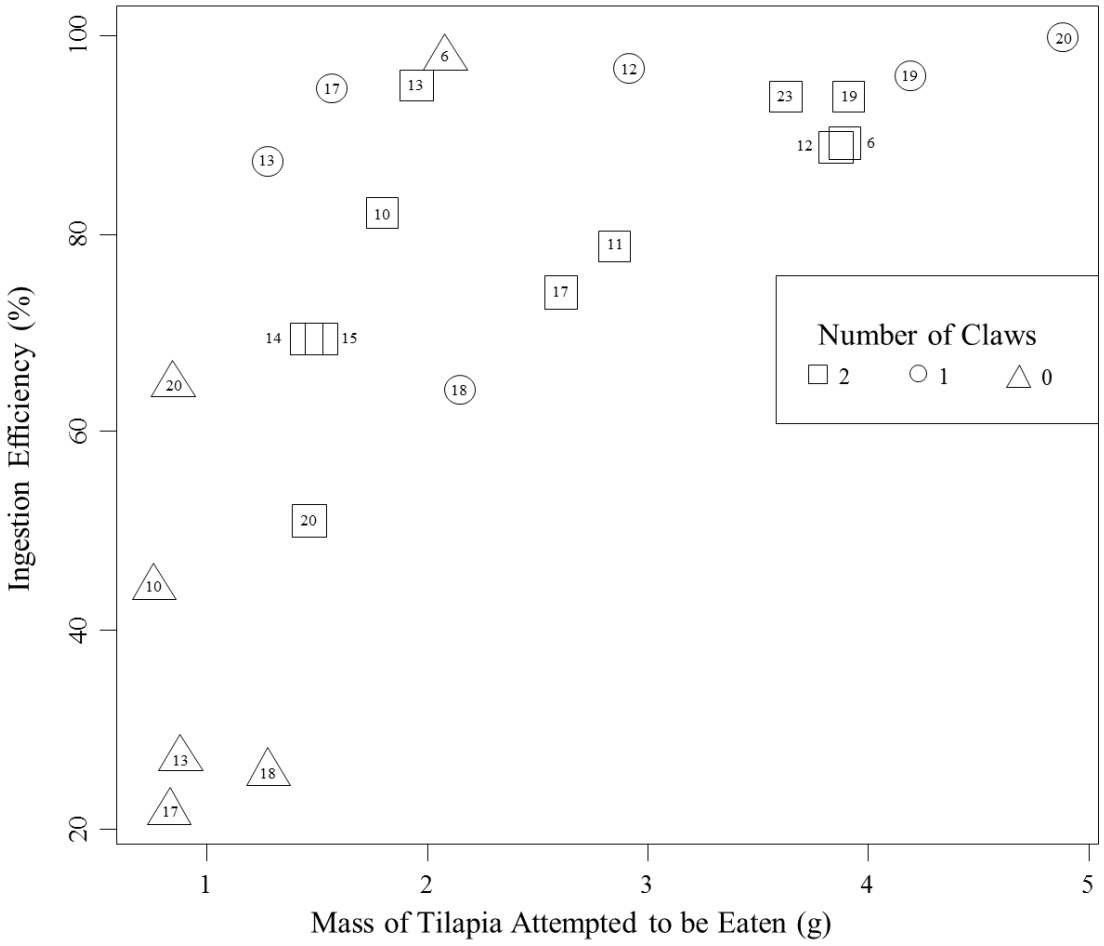

Figure 3.5. The ingestion efficiencies of stone crabs with the corresponding mass of tilapia the crab attempted to eat. The number within each data point represents the crab ID while the point shape represents the number of claws present for each measurement period.

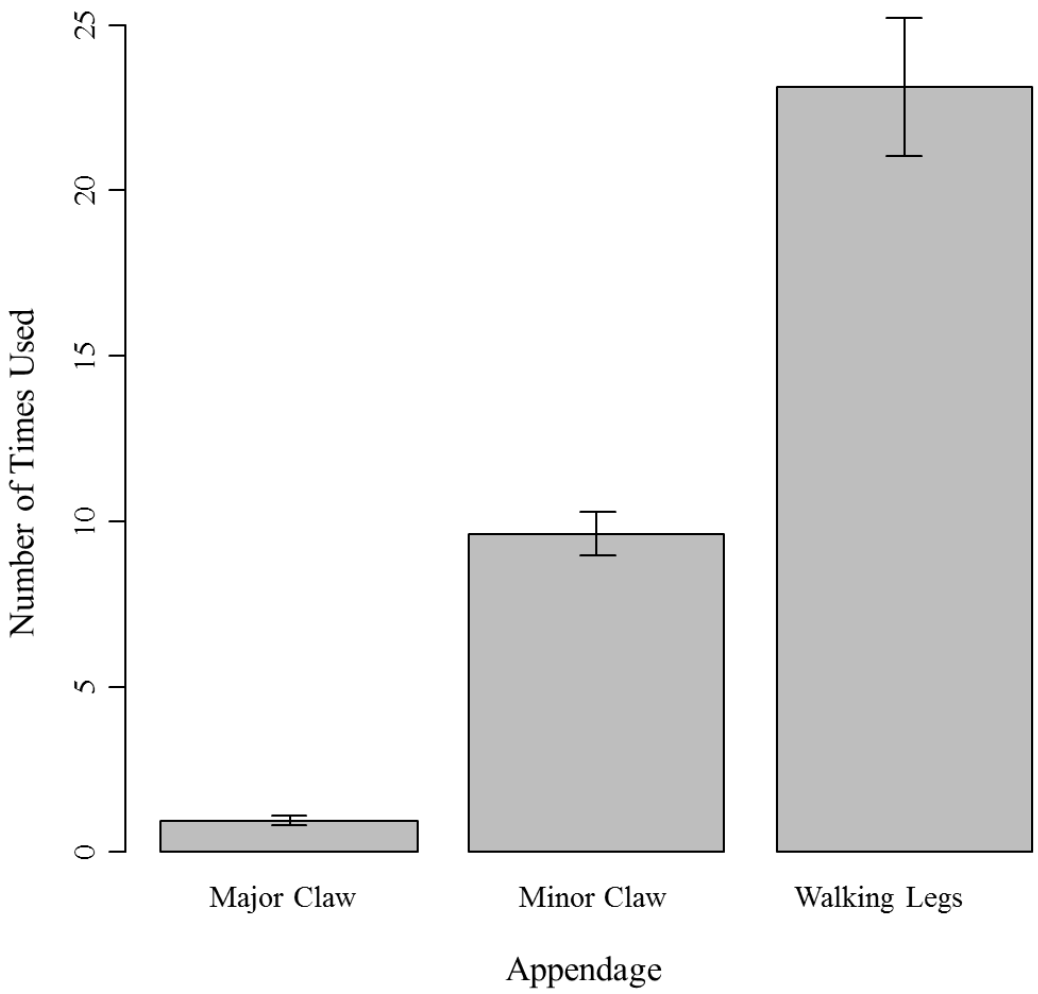

Figure 3.6. The number of times each appendage was used to manipulate the oyster during feeding. Each bar includes all three replicates from each of the five crabs. Error bars represent ± standard error about the mean.

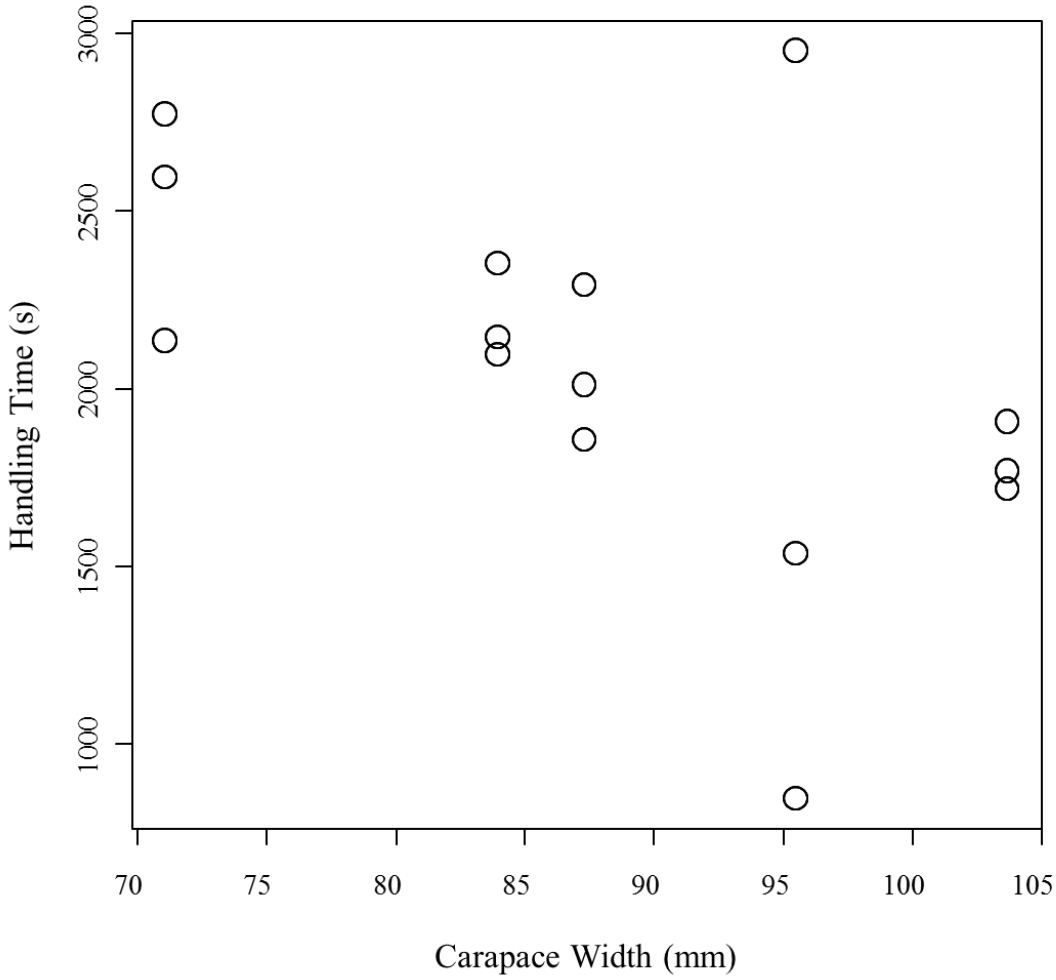

Figure 3.7. The handling time of stone crabs on single oysters (85.3 ± 10.7mm) with the corresponding carapace width.

CHAPTER 4

DISCUSSION

As expected, I found mass-specific respiration rates increased with water temperature, dissolved O_2, and claw loss. Increased mass-specific respiration rates following claw loss may have come from the energetic cost of regenerating a claw or may be an artifact of removing a large portion of the body that has a relatively low energetic maintenance cost. It is important to note that respiration rates here reflect the combined respiration of crabs and the bacterial community. Independent measurements of oxygen loss in the absence of crabs suggests that up to 47% of the respiration reported here may be attributable to bacteria. In the consumption experiment I found that crabs again behaved as expected and consumed more oysters as the crabs' size and the water temperature increased. The influence of claw loss on oyster consumption was not examined in this study since Hogan & Griffen (2014) previously demonstrated that stone crabs missing a claw consume 50% fewer hard-shelled bivalves. However, as a part of the temperature-respiratory experiment I found that the crabs consume more fish flesh after claw loss, similar to *C. pagurus* (Patterson et al. 2009). This finding suggests that if easily-consumed food (i.e., non-hard shelled prey) is readily available, stone crabs will meet the increased energetic demands of claw regeneration by increasing food consumption. Although the ingestion efficiency of clawless crabs was numerically lower than that of the 2- or 1-clawed crabs, it was not significantly lower, possibly due to low power resulting from small sample sizes. It appears that use of walking legs may be the primary reason that ingestion efficiency did not change with the loss of a single claw.

Stone crabs used their walking legs in food manipulation far more than expected, perhaps due to the relatively large and cumbersome claws of this species.

The imbalance in energy expenditure (respiration) and intake (oyster consumption) with water temperature shown in this study suggests a potential temperature threshold for the stone crab determined by energetics. I derive a rough estimate of this threshold using respiration and consumption results over the range of temperatures presented here. To do this, I made some unit conversions to put energy expenditure and intake into comparable units. For energy expenditure, I first converted the respiration rates from the temperature-respiratory experiment (ml O_2 g^{-1} crab h^{-1}) to mg O_2 g^{-1} crab $week^{-1}$. Consistent with our observations while capturing experimental animals, I next assume that stone crabs are only active at night, which I define as 8 hours per day. I therefore estimated total metabolic expenditure by assuming that active respiration by stone crabs is 3X higher than passive respiration, consistent with relative active and passive rates of other crab species (Wallace 1972). I then converted the total (i.e., active + passive) respiration rates from mg O_2 g^{-1} crab $week^{-1}$ to calories g^{-1} crab $week^{-1}$ using the proportion of fat, protein, and carbohydrates in the crabs' primary diet, the eastern oysters *Crassostrea virginica* (16.86% fat, 56.31% protein, and 26.82% carbohydrates [USDA 2016]), and using conversion rates of 3.28, 3.25, and 3.53 cal mg^{-1} O_2 consumed for fat, protein, and carbohydrates metabolized, respectively (Elliot & Davison 1975). Finally, I converted energetic equivalents in cal g^{-1} crab $week^{-1}$ to Joules g^{-1} crab $week^{-1}$.

For the consumption half of the calculations, I first applied the ingestion efficiency of 2-clawed crabs (E_I = 80.44%) to the difference in oyster mass in between

the beginning and end of the experimental period in the consumption rate experiment to determine the mass of oysters (g oyster $week^{-1}$) that was actually ingested. I then standardized oyster consumption rates across crab size into units of g oyster g^{-1} crab $week^{-1}$. Our consumption experiment enclosed crabs in cages where they had access to excess food, refuge via a false burrow, and no predation risk. The ~80% of body mass consumed by these crabs weekly therefore represents maximum possible consumption rates under ideal conditions. I then converted the mass of oyster consumed into the energy intake using 0.51 kcal g^{-1} oyster (USDA 2016) assuming assimilation efficiency was 100% and consistent across temperatures (Giguere 1981). Finally, I converted kcal g^{-1} crab $week^{-1}$ to Joules g^{-1} crab $week^{-1}$. Although the calculations described above contain many assumptions, they provide the following general estimates for relative changes in energy expenditure and intake with temperature variation. For every 10°C decrease in ambient temperature, the energy intake is reduced by roughly 550 Joules g^{-1} crab $week^{-1}$ while the energy expenditure only reduces by 70 Joules g^{-1} crab $week^{-1}$. This suggests that at low temperatures, energy expenditure will outpace energy intake, creating a potential temperature threshold for the stone crab.

While the above calculations provide a mechanistic basis for the lower temperature threshold of stone crabs, they do not identify a specific temperature of a tipping point between the rate of energy expenditure and energy intake. In preliminary experiments, I observed reduced feeding in waters below 15°C, and inhibited claw use has been demonstrated in stone crabs in waters below 8°C (Brown et al. 1992). At the northern edge of the stone crab's range, summertime temperatures are sufficiently warm that energy intake exceeds energy expenditure, while the reverse is likely true at

wintertime temperatures. The specific northern extent of stone crabs may therefore be determined by degree days (i.e., the cumulative average of daily temperatures, Kurata 1961). The stone crab is expanding its range northward (Rindone & Eggleston 2011); however, the rate at which this will occur with further warming likely depends on the balance of energy intake and expenditure at different temperatures. Further research is required to determine the degree days that provide the precise tipping point in the energetics of this species.

Our results also have implications for the stone crab fishery. The claw-only stone crab fishery aims to lessen the impact on populations because harvested individuals are not necessarily killed. However, our results suggest that stone crabs may struggle to cope with the combined effects of increasing water temperatures and fishery-style claw loss, especially in areas that are O_2 depleted. Though I did not manipulate O_2 levels, I found that low dissolved O_2 and increased temperature were of similar importance in influencing respiration. This suggests that environmental factors like dissolved O_2 concentrations may influence the stone crab fishery. Yet, fishing regulations for this stock do not incorporate dissolved O_2 concentrations. Low O_2 levels could be a problem in some regions on the Florida coast. For instance, there is concern in Florida for the pollution in Lake Okeechobee draining into the Caloosahatchee River Estuary. Agricultural production and urban development in the watershed load nitrogen and phosphorus into the estuary, contributing to an increasing frequency of eutrophication (Knight & Steele 2005). Between the 2003-04 and 2009-10 fishing seasons, the region which contains the Caloosahatchee River Estuary pulled the highest number of traps by at least 1.2 million each fishing season, while only yielding the highest landings in one of

those seven seasons (Muller et al. 2011). The eutrophication and O_2 depletion resulting from nutrient loading in this area may potentially contribute to the decreased catch per unit effort in the Southwest region compared to neighboring regions.

Eutrophication and O_2 depletion are issues that extend to environmental systems beyond southern Florida and the stone crab. In the United States the number and intensity of hypoxic and anoxic waters, harmful algal blooms, and eutrophic areas has increased in coastal waters since the early 1990s (Scavia & Bricker 2006). Globally the trend is the same; the first comprehensive list of hypoxic zones identified 45 areas worldwide (Diaz & Rosenberg 1995) while thirteen years later the list has grown to 169 hypoxic areas with an additional 233 areas of concern for eutrophication (Selman et al. 2008). Although underreporting in certain parts of the world cause these numbers to be conservative, in general, coastal waters are experiencing lower levels of dissolved O_2. However, hypoxia tends to be ignored until higher-level organisms, often commercially important organisms, are affected (Diaz & Rosenberg 2008). Loss of commercial stocks in the Chesapeake Bay, Gulf of Mexico, and Baltic Sea are estimated as high as 6, 17, and 106 thousand metric tons of carbon per year, respectively, due to severe seasonal hypoxia (Moeller et al. 1985, Diaz & Schffner 1990, Rabalais & Turner 2001, Diaz & Rosenberg 2008). Hypoxia and the issues associated with low O_2 waters affect most organisms within each system, not just those that are of commercial importance. The results presented here suggest that hypoxia could also be highly detrimental to stone crab energetics and thus to the stone crab fishery.

In summary, I have shown that stone crab respiration increases with dissolved O_2, water temperature, and claw loss. Food consumption rates also increase with water

temperature, crab size, and crabs will increase consumption following claw loss if easily consumed (i.e., soft) food is readily available. Although higher water temperatures led to both increased respiration and food consumption, the rate of change in food consumption with temperature is much greater than the rate of change of respiration. Lastly, ingestion efficiency of soft tissue did not significantly decrease as crabs lost claws, likely due to the compensatory use of walking legs in manipulating food.

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